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Genetic Parameters of Growth Traits and Stem Quality of Silver Birch in a Low-Density Clonal Plantation

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Received: 4 December 2017; Accepted: 22 January 2018; Published: 23 January 2018

Abstract: Silver birch (*Betula pendula* Roth) is productive on abandoned agriculture land, and thus might be considered as an option for profitable plantation forestry. Application of the most productive genotypes is essential. However, information about genetic gains in low-density plantations is still lacking. A 40-year-old low-density (400 trees ha⁻¹) plantation of 22 grafted silver birch plus-tree clones growing on former agricultural land in the central Latvia was studied. Although grafted plantations are not common in commercial forestry, the trial provided an opportunity to assess genetic parameters of middle-aged birch. The plantation that had reached the target diameter for final harvest (DBH (diameter at breast height) = 27.7 ± 5.5 cm) had an 85% survival rate, and stemwood productivity was 5.25 m³ ha⁻¹year⁻¹. Still, rootstock × scion interaction and cyclophysis might have caused some biases. Broad-sense heritability (H^2) ranged from 0.02 for probability of spike knots to 0.40 for branch angle. Estimated H^2 for monetary value of stemwood was 0.16. In general, the correlations between growth and stem quality traits were weak, implying independent genetic control, though branchiness strongly correlated with diameter at breast height. The monetary value of stemwood strongly correlated with productivity traits. The observed correlations suggested that productivity and stem quality of birch might be improved simultaneously by genetic selection.

Keywords: mature *Betula pendula*; clonal forestry; tree breeding; target diameter

1. Introduction

The economic importance of plantation forestry on abandoned agricultural land is increasing [1]. Application of the most productive genotypes is essential for profitability of such plantations [2]. In the Baltics, hybrids of *Populus* L. are highly productive, yet they are strongly damaged by wildlife and require continuous protection [3]. Silver birch (*Betula pendula* Roth) has substantially lower environmental risks, yet is productive on agricultural land [4], and might be considered as an alternative. When appropriately cultivated (e.g., in a low-density plantation), birch can rapidly reach target diameter, reducing rotation time and increasing profitability of a plantation [4]. However, information about very low-density plantations is lacking.

Many traits including productivity and branchiness are highly heritable, emphasizing the potential to improve growth and stem quality [5,6]. Nevertheless, some traits can have common genetic control [7], which might differ regionally [4,6]. Furthermore, genetic parameters, such as heritability or genotypic coefficients of variation at final-harvest age, are unknown for silver birch. Genetic gains can be estimated theoretically from young trials, but the information about actual realization of these gains at mature age is available for tropical tree species [8,9], although is still lacking for silver birch.

The aim of this study was to estimate genetic parameters at the final-harvest age for stem quality and growth traits of silver birch clones planted in a low-density (400 trees ha⁻¹) plantation on former

agricultural land. We hypothesized that the gain of productivity and stem quality of silver birch in a low-density plantation can be substantially improved by tree breeding.

2. Materials and Methods

The study site was located in the central part of Latvia (57°32' N, 24°44' E). The topography was flat (elevation < 100 m above sea level). The mean annual temperature was 6.2 °C; the mean monthly temperature ranged from 4.6 °C to 17.5 °C in February and July, respectively. The mean annual precipitation was ca. 690 mm.

The trial was established in 1972 on agricultural land, equivalent to *Oxalidos* stand type with mesotrophic loamy soil. One year after grafting, clones of 22 birch plus-trees from the central part of Latvia (56°37'–57°28' N; 24°50'–26°24' E) were planted in a 5 × 5 m grid (400 trees ha⁻¹) as single-tree plots in 13–56 randomly distributed replications. Clones were randomized spatially all over the planting site. Initially, the plantation was intended as a seed orchard, but abandoned soon thereafter; hence no management, except some initial cleaning, was performed. The area of the plantation was 1.8 ha (720 planting spots).

At the age of 40 years in 2012, for each tree (1) diameter at breast height (DBH; cm); (2) height (m); (3) height of the lowest living branch (m); (4) mean branch angle (°); (5) mean projection of crown (MPC; m); (6) occurrence of spike knots; (7) double tops; and (8) stem cracks (present/absent), and arbitrary scores using 6-point-scales of (9) stem straightness and (10) branchiness were measured.

Data analysis was conducted in program R, v. 3.3. [10]. For each tree, the volume of stemwood assortments was calculated according to the model by Ozolins [11]. Wood defects and stem quality traits were considered when determining the structure of stemwood assortment (according to the practices of commercial forestry in Latvia). According to the estimated volume of assortments, the monetary value of stemwood (MV) of each sampled tree was calculated as an integrative parameter. Prices of different assortments according to top diameter, as used in the calculation of MV, were 20, 26, 45, 60, and 70 euro m⁻³ for firewood (<13 cm), pulpwood (<13 cm), logs 14–18 cm, logs 19–25 cm, and logs >26 cm, respectively.

Heritability coefficients H^2 (broad-sense individual-tree heritability) for the studied variables were calculated [7]:

$$H^2 = \sigma_G^2 / \sigma_P^2, \quad (1)$$

where σ_G^2 is genotypic variance and σ_P^2 is phenotypic variance constituted of genotypic and environmental variance.

Genetic gain was estimated according to formula [7]:

$$R = S \cdot H^2, \quad (2)$$

where S is selection differential, which is the mean phenotypic value of the selected clones expressed as a deviation from the trial mean. For each variable, superiority of the top three clones against trial mean was assessed.

Genotypic and phenotypic clone mean Pearson correlations were estimated for the studied variables [7]. Genotypic correlations between the traits were calculated using the formula:

$$r_G = \frac{\sigma_{G(x,y)}}{\sqrt{\sigma_{G(x)}^2 \sigma_{G(y)}^2}}, \quad (3)$$

where $\sigma_{G(x,y)}$ is the genetic covariance between traits x and y ; $\sigma_{G(x)}^2$ and $\sigma_{G(y)}^2$ are the genotypic components of variance estimated for the traits. Standard errors for the genotypic correlation estimates were obtained with the delta method [12].

Genotypic coefficients of variation (CVg), describing the extent of genetic variability of a variable in relation to the mean of trial, were calculated as:

$$CVg = \sqrt{\sigma_G^2} \cdot 100 / \bar{x}, \quad (4)$$

where \bar{x} is the phenotypic mean.

The corresponding components of genotypic and environmental variance were extracted using a random model:

$$y_{ij} = \mu + c_i + \varepsilon_{ij}, \quad (5)$$

where y_{ij} is observation of each trait of the ij th tree, μ is the overall mean, and c_i is the random clone effect. For the quantitative variables (e.g., DBH, tree height), a linear mixed model was used. For the binomial variables (e.g., survival, probability of cracks, etc.), a generalized linear mixed model applying binomial residual distribution and “logit” link function was fitted. For both models, R package lme4 was used [13]. For stem straightness and branchiness, ordinal logistic regression was applied [14] using R package ordinal [15]. The environmental variance of the link functions was determined as $\pi^2/3$, or 3.29. Genetic covariance $\sigma_{G(x,y)}$ between any two traits x and y was estimated using function varcomp in package lme4.

3. Results

The studied plantation had 84.4% survival at the age of 40 years. The mean (\pm standard deviation) height and DBH of trees was 26.2 ± 2.2 m and 27.7 ± 5.6 cm, respectively. The total standing stemwood volume of the plantation was $210 \text{ m}^3 \text{ ha}^{-1}$, and the mean annual stemwood increment was $5.25 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$. Accordingly, MV was estimated ca. $9600 \text{ euro ha}^{-1}$, mainly contributed by the logs of smaller, medium, and large dimensions (44%, 25%, and 21%, respectively).

The estimated H^2 and CVg differed among the variables (Table 1). The highest heritability was estimated for branch angle, mean projection of crown (MPC), branchiness, and stem straightness ($0.40 \leq H^2 \leq 0.29$, respectively), while the lowest heritability was estimated for survival, probability of spike knots and cracks (<0.08). Intermediate $H^2 = 0.16$ for MV was similar to commonly reported tree height, height of the lowest living branch, and DBH (0.14, 0.14, and 0.21, respectively). The CVg of the quantitative variables ranged from 3.2% to 21.8% for tree height and MV, respectively (Table 1). For DBH and height of the lowest living branch, intermediate genotypic variation (ca. 9%) around the phenotypic mean was estimated, while it was higher for branch angle and MPC at -14.8% and 19.2% , respectively. For each variable, selection of top three clones resulted in 3.8%, 0.6%, and 2.7% genetic gain for DBH, tree height, and MV, respectively (Table 2).

The estimated genotypic correlations among the studied variables were similar to phenotypic clone mean Pearson correlations (Table 3); the latter are described. Correlations among tree height, DBH, and MV were high ($r > 0.63$); nevertheless, DBH and MV ($r > 0.66$) correlated with MPC. Branchiness correlated with DBH ($r = 0.79$), yet not with tree height (p -value = 0.41). Moderate to strong ($0.30 < |r| < 0.78$) negative correlations were observed between height of the lowest living branch and DBH, double tops, stem straightness, branchiness, and MPC. Occurrence of double tops showed moderate to strong correlations with stem straightness, branchiness, and MPC ($r = 0.70, 0.67$, and 0.56 , respectively), but a negative correlation ($r = -0.68$) with occurrence of spike knots. Mostly, weak and non-significant correlations were observed between the occurrence of stem cracks as well as branch angle and other variables.

Table 1. Statistics, coefficients of heritability (H^2), and genotypic variation (CV_g , %) of the morphometric variables (traits), and monetary value of 40-year-old grafted birch plus-trees from the low-density plantation. The monetary value of stemwood was calculated considering stem quality.

	Mean	Min	Max	Standard Deviation	Heritability Coefficient $H^2 \pm$ Standard Error	Genotypic Coefficient of Variation $CV_g \pm$ Standard Error (%)
Quantitative variables						
Stem diameter at breast height, cm	27.7	14.2	45.8	5.6	0.21 ± 0.06	9.5 ± 1.5
Tree height, m	26.2	15.3	31.6	2.2	0.14 ± 0.05	3.2 ± 0.5
Height of the lowest living branch, m	11.2	1.8	18.0	2.7	0.14 ± 0.05	9.3 ± 1.4
Branch angle, °	43.2	15.0	80.0	10.4	0.40 ± 0.08	14.8 ± 2.3
Mean projection of crown, m	2.9	1.1	6.3	0.8	0.39 ± 0.08	19.2 ± 3.0
Monetary value of stemwood, euro	28.2	3.7	95.4	14.6	0.16 ± 0.05	21.8 ± 3.4
Qualitative variables						
Survival, % of trees *	84.4	59.6	100.0	-	0.08 ± 0.03	-
Spike knot, % of trees *	23.2	5.2	42.8	-	0.02 ± 0.02	-
Double tops, % of trees *	34.9	6.0	75.1	-	0.14 ± 0.05	-
Stem straightness, score *	3.2	2.5	4.7	-	0.29 ± 0.07	-
Branchiness, score *	3.3	2.5	5.3	-	0.33 ± 0.08	-
Stem cracks, % of trees *	24.9	0.0	50.3	-	0.08 ± 0.03	-

* Mean values for clones.

Table 2. Clone means with standard errors (SEs) for studied traits.

Clone	Number of Trees	Survival, %	Diameter at Breast Height, cm		Height, m		Height of the Lowest Living Branch, m		Branch Angle, °		Mean Projection of Crown, m		Monetary Value of Stemwood, Euro		Stem Straightness, Score		Branchiness, Score		Double Tops, % of Trees	Spike Knots, % of Trees	Stem Cracks, % of Trees
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
1	36	79.4	26.6	0.7	25.7	0.3	11.5	0.4	38.8	0.6	2.7	0.1	22.6	1.4	3.1	0.1	3.3	0.1	16.7	27.8	41.7
2	36	86.9	29.9	0.7	27.1	0.3	11.6	0.3	40.4	0.9	2.9	0.1	34.5	2.2	3.0	0.1	3.2	0.1	11.1	36.1	33.3
3	21	78.2	31.6	1.2	26.0	0.5	8.8	0.6	38.6	1.5	3.8	0.2	36.2	2.6	4.3	0.2	4.5	0.3	66.7	19.0	4.8
4	20	83.3	33.2	0.9	25.7	0.4	8.3	0.3	41.8	1.3	4.5	0.2	36.4	2.1	4.7	0.2	5.3	0.2	75.0	5.0	5.0
5	16	92.3	30.9	1.2	27.1	0.5	11.5	0.8	49.7	1.9	3.5	0.2	35.3	3.7	3.4	0.2	3.9	0.3	37.5	25.0	18.8
6	28	91.9	29.1	1.0	26.5	0.5	10.6	0.5	42.9	1.7	3.3	0.2	31.8	3.1	3.8	0.2	3.7	0.2	53.6	21.4	21.4
7	41	90.8	27.5	0.9	27.4	0.3	11.8	0.4	43.3	1.2	3.1	0.1	28.4	2.3	3.3	0.1	3.3	0.1	56.1	24.4	0.0
8	24	81.8	22.2	1.0	24.3	0.4	11.9	0.6	44.8	1.8	2.3	0.1	16.5	2.5	3.2	0.2	2.5	0.1	20.8	37.5	8.3
9	16	91.4	28.6	2.0	26.1	0.5	9.5	0.6	38.1	2.1	3.3	0.3	27.4	3.5	3.8	0.2	3.8	0.4	62.5	12.5	12.5
10	16	68.1	23.9	1.1	23.7	0.9	10.7	0.7	38.8	1.6	2.3	0.1	18.7	2.5	3.3	0.2	2.8	0.2	25.0	18.8	43.8

Table 2. Cont.

Clone	Number of Trees	Survival, %	Diameter at Breast Height, cm		Height, m		Height of the Lowest Living Branch, m		Branch Angle, °		Mean Projection of Crown, m		Monetary Value of Stemwood, Euro		Stem Straightness, Score		Branchiness, Score		Double Tops, % of Trees	Spike Knots, % of Trees	Stem Cracks, % of Trees
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
11	35	88.7	25.7	0.6	25.7	0.4	11.2	0.4	38.0	1.8	2.6	0.1	22.0	1.3	3.3	0.2	3.4	0.1	57.1	14.3	14.3
12	39	88.3	24.2	0.7	24.9	0.3	11.7	0.4	38.5	1.0	2.6	0.1	19.6	1.7	3.4	0.2	3.1	0.1	41.0	15.4	20.5
13	18	90.2	23.9	1.3	26.3	0.8	12.2	0.6	37.8	1.0	2.2	0.2	20.7	3.4	2.8	0.2	2.7	0.2	33.3	11.1	16.7
14	12	89.2	27.8	1.4	25.5	0.7	10.3	0.6	48.8	3.1	3.0	0.2	27.3	4.4	3.8	0.3	3.4	0.2	33.3	41.7	41.7
15	29	100.0	30.4	0.6	26.7	0.3	9.3	0.5	37.6	1.0	3.3	0.1	34.5	2.1	2.7	0.1	3.5	0.1	55.2	6.9	48.3
16	23	59.6	28.8	1.4	27.0	0.5	11.9	0.5	41.1	1.9	2.6	0.1	32.8	3.5	2.9	0.2	3.0	0.2	43.5	13.0	30.4
17	33	69.0	28.6	0.6	26.8	0.2	11.7	0.4	61.5	2.0	3.4	0.1	30.8	1.7	2.6	0.1	3.1	0.1	6.1	33.3	30.3
18	46	82.7	28.4	0.8	27.2	0.2	12.3	0.5	57.8	1.5	2.8	0.1	31.7	2.4	3.0	0.1	2.8	0.1	26.1	23.9	28.3
19	36	87.3	28.2	1.0	26.0	0.3	11.1	0.4	41.4	1.0	2.6	0.1	30.8	2.8	2.5	0.1	2.9	0.1	16.7	22.2	41.7
20	28	81.1	24.8	0.7	26.0	0.4	10.9	0.6	41.1	0.9	2.5	0.1	21.2	2.0	3.3	0.2	3.0	0.1	28.6	28.6	25.0
21	31	94.4	26.6	0.8	26.1	0.3	12.8	0.4	36.5	1.3	2.2	0.1	26.2	2.2	2.5	0.2	2.7	0.2	9.7	32.3	19.4
Ka1	14	82.9	33.3	2.0	27.4	0.5	11.0	0.6	49.3	2.5	3.8	0.3	42.0	6.8	3.6	0.2	4.1	0.3	28.6	42.9	50.0
Total	598	84.4	27.7	0.2	26.2	0.1	11.2	0.1	43.2	0.4	2.9	0.0	28.2	0.6	3.2	0.0	3.3	0.0	34.9	23.2	24.9

Table 3. Genotypic correlations (standard errors by delta method in brackets) in the upper diagonal part and phenotypic clone mean Pearson correlations (significant correlations with $p \leq 0.05$ in bold) in the lower diagonal part (*—calculation stopped due to infinite likelihood).

	Tree Height	Stem Diameter at Breast Height	Stem Cracks	Height of the Lowest Living Branch	Branch Angle	Double Tops	Spike Knots	Stem Straightness	Branchiness	Mean Projection of Crown	Monetary Value of Stemwood
Tree height	1	0.65 (0.16)	0.02 (0.30)	0.14 (0.27)	0.43 (0.21)	0.03 (0.27)	0.17 (0.45)	-0.16 (0.25)	0.16 (0.25)	0.35 (0.22)	0.79 (0.11)
Stem diameter at breast height	0.63	1	0.11 (0.29)	-0.56 (0.19)	0.23 (0.23)	0.35 (0.23)	-0.23 (0.43)	0.44 (0.20)	0.79 (0.10)	0.86 (0.07)	0.93 (0.03)
Stem cracks	0.03	0.10	1	-0.11 (*)	0.08 (0.02)	-0.68 (0.20)	0.38 (0.44)	-0.60 (0.21)	-0.30 (0.27)	-0.20 (0.27)	0.47 (*)
Height of the lowest living branch	0.17	-0.51	0.07	1	0.29 (0.23)	-0.75 (0.13)	0.90 (0.37)	-0.76 (0.12)	-0.85 (0.24)	-0.77 (0.11)	-0.32 (0.25)
Branch angle	0.36	0.22	0.15	0.25	1	-0.37 (0.22)	0.67 (0.31)	-0.09 (0.23)	-0.25 (0.07)	0.27 (0.22)	0.29 (0.23)
Double tops	0.05	0.35	-0.51	-0.69	-0.34	1	-1.19 (0.35)	0.78 (0.12)	0.74 (0.13)	0.60 (0.17)	-0.10 (*)
Spike knot	0.06	-0.07	0.29	0.40	0.46	-0.68	1	-0.47 (0.43)	-0.64 (0.40)	-0.35 (0.22)	0.06 (0.48)
Stem straightness	-0.15	0.42	-0.41	-0.71	-0.08	0.70	-0.15	1	0.87 (0.07)	0.60 (0.14)	0.12 (0.25)
Branchiness	0.19	0.79	-0.22	-0.78	-0.05	0.67	-0.26	0.82	1	0.93 (0.03)	0.28 (0.28)
Mean projection of crown	0.36	0.86	-0.15	-0.71	0.26	0.56	-0.16	0.70	0.93	1	0.65 (0.14)
Monetary value of stemwood	0.74	0.93	0.32	-0.30	0.28	0.14	0.03	0.14	0.54	0.66	1

4. Discussion

The calculated H^2 (Table 1) implied potential for substantial improvement of productivity and stem quality, hence yields of birch plantations by tree breeding [5]. Nevertheless, H^2 of the variables differed (Table 1), implying unequal potential for the improvement of the traits [7]. Branch angle, branchiness, projection of crown, and stem straightness, which largely influence timber quality [2], were highly heritable and had intermediate CVg (Table 1), implying potential for considerable improvement [7]. High CVg was also observed for MV (21.8), indicating potential financial benefits from breeding. Nevertheless, strong correlation between branchiness and DBH, MPC, and stem straightness indicated possible negative effects on stem quality when selecting fast growing trees with straight stems (Table 3). Additionally, height of the lowest living branch had significant negative correlations with the same variables, supporting the abovementioned consideration. Earlier studies reported a significant moderate correlation between DBH and number of branches [5,16]. Significant negative genotypic correlation between productivity traits and stem straightness (r_G ranging from -0.45 to -0.72) was noticed in Sweden [16]. However, other stem quality traits such as spike knots, stem cracks, and double tops did not show significant relation to productivity traits and MV, suggesting the possibility for simultaneous improvement [16,17].

The heritability of survival was low (Table 1), suggesting the prevailing effect of the micro-site conditions, as shown by Stener and Jansson [16] for birch in Sweden. Environmental factors can strongly affect performance of the species, masking the genetic effect and resulting in low heritability parameters [6]. The estimated genetic parameters (Table 1) might have been already affected by the pre-selection of planting material (plus-trees) with improved branching and stem properties, as a seed orchard was initially intended. Although the utilization of grafted silver birch is not a common practice in commercial forestry, the trial provided information about genetic parameters at middle age that has not been previously published. This might have caused some imprecisions in genetic parameters due to uncontrolled rootstock \times scion effect. Although the issue has been scarcely studied for forest trees [18], for loblolly pine, the rootstock \times scion effect has been negligible compared to the effects of clone and site factors [19]. This was also supported by good survival of grafts indicating compatibility between rootstock and scions. The negative effect of cyclophysis due to different biological ages of rootstock and scion [20–23] appeared insubstantial, as indicated by the productivity of the plantation. Similarly, a weak effect of cyclophysis on growth and survival of vegetatively propagated silver birch has been shown in boreal conditions [24,25]. Still, grafts might have lower branchiness and branch thickness [26].

The single-tree-plot design of the plantation might have also affected genetic parameters of the traits, as the measurements from such plots are influenced by competition among different genotypes [27]. However, low planting density likely had postponed the onset of inter-tree competition, therefore reducing exaggeration of the genotypic variance of growth traits [5,16,28]. Hence, the estimated H^2 and CVg were somewhat lower than reported in earlier studies, in which H^2 ranged 0.07–0.56 for tree height, and 0.11–0.59 for DBH, while CVg for the respective traits has been reported to range between 5 and 14, and between 9 and 21, respectively [5,16,28]. Still, heritability of height and DBH varies widely among different trials [16]. Considering varying genetic control of the studied traits, H^2 and CVg of MV were intermediate (0.16 and 21.8), as similarly observed in Sweden [5].

For silver birch, genetic gains of around 10% for height and 20% for DBH of the top 10% clones at the age of 7–11 years are reported [5,16], while corresponding realized gains in our study site at the moment of possible final-harvest was around 17 and 5 times lower, respectively. This may imply weak age-age correlations, as well as reflect lower heritability and high variability due to strong environmental effects (Table 2). However, earlier measurements from the studied trial were not available for comparison.

The studied plantation appeared ready for the final harvest already at the age of 40 years. Higher productivity (up to $8.90 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ [29] vs. $5.25 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ in studied trial) and good stem quality might be achieved in conventional plantations with higher planting densities [30,31], although

increasing planting distance does not influence the height growth [31]. Nevertheless, decreased competition and application of the pre-selected planting material apparently improved the assortment structure of the studied birch, shifting its distribution towards the higher value, thus suggesting efficiency of the low-density clonal plantation for the production of solid wood and possible further economic improvement in a low-density short-rotation plantation. Together with selected planting material, reduced establishment costs with wider spacing might be a strong driving factor for choosing lower planting densities. Increased value does not only result from increases in volume production, but also from improved stem quality leading to more valuable logs [9]. Besides, breeding effect on productivity might not fully express in dense stands, since birch maintain vigorous growth when presented with low within-stand competition [4].

5. Conclusions

Although the utilization of grafted silver birch is not a common practice in commercial forestry, the studied forty-year-old, low-density grafted clonal plantation appeared efficient for the production of solid wood. Considering heritability and genetic gains of the studied traits, the gain of birch plantations might be substantially improved by breeding. The non-significant correlations between stem quality and dimensions of trees suggested that the traits could be improved simultaneously. However, the strong correlation between branchiness and DBH implied that stem quality would be reduced when selecting for productivity. Still, rootstock \times scion interaction and cyclophysis effects are uncertain and might be potentially significant. Considering the potential for strong environmental effects on the performance of birch, verification of the results in diverse growing conditions is required.

Acknowledgments: The study was carried out in accordance to contract No. 1.2.1.1/16/A/009 between “Forest Sector Competence Centre” Ltd. and the Central Finance and Contracting Agency, funded by the European Regional Development Fund (ERDF) within the framework of the project “Forest Sector Competence Centre”. We acknowledge JSC “Latvijas valsts meži” for information about standing stock of the conventional stands. Jānis Donis and Virgilijus Baliuckas helped with data analysis.

Author Contributions: Ā.J. conceived the original research idea. All authors contributed to the experimental design. J.K. and J.J. were responsible for data collection. Ā.J., R.M., and P.Z. analyzed the data. A.G., Ā.J., R.M., and P.Z. wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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